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Equalization of Net Income in a Non-Cooperative Evolutionary Game, with Special Reference to Evolution of Tax Payment in Cellular Slime Molds

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ABSTRACT

Evolution of resource allocation strategies is studied by using a simple mathematical model. Considered are the allocation of cells to stalks and spores by cellular slime molds, that of reproductive investment to daughters and sons by aphids, and that of reproductive investment to cleistogamic and chasmogamic flowers by plants. Evolutionarily stable strategies, which are equivalent in this case to the Nash equilibrium strategies in non-cooperative games, are obtained. It is shown that, at the evolutionary equilibrium, amount of resource allocated to a component (spores, sons or non-dispersing offspring) is equalized among individuals, even if they have different amount of total resource. We discuss the properties common to all these resource allocation problems and propose "the law of equalization in net income".

INTRODUCTION

One of the everlasting problems in human social interaction is the problem of taxation. How much should an individual of certain income be taxed? Many governments in the world employ a mixed strategy of taxing; an income tax and a sales tax. In the income tax, taxation rate to an individual is determined on the basis of his total income and is usually an increasing function of it. In sales tax, any kind of consuming activity is taxed by some fixed rate which is independent of individual's total income. In addition, some governments employ, or try to employ, a poll

tax in which every citizen must pay some fixed amount of tax irrespective of his total income.

We here study the evolution of tax payment by cellular slime molds. The cellular slime mold is one of the simplest multi-cellular organisms. The life history of it consists of two distinctive phases; "free-living" and "aggregating". Spores germinate to free-living amoeboid cells, which grow by phagocytosis and multiply by binary fission under a suitable food supply (free-living phase; Bonner, 1967). If these cells become starved, they aggregate to form a pseudoplasmodium, which moves to a suitable location and develops into a fruiting body (aggregating phase; Bonner, 1947, 1967). Cells differentiate into two types of cells in the fruiting body. In most species such as *Dictyostelium discoideum*, about two-thirds of cells become spores, which germinate to amoeboid cells of the next generation (Bonner, 1978). The remainder, called "stalk" cells, support and elevate spores but leaves no descendants for the next generation. The stalk may promote the dispersal of spores, which adhere to the legs or carapaces of passing soil invertebrates (Bonner, 1982 a, b).

In nature, a fruiting body of the cellular slime mold is not necessarily composed of a single clone (Buss, 1982). Spores disperse and amoeboid cells move around and intermingle. Thus several clones may coexist in close proximity, and further, they may co-aggregate to form a fruiting body. In the fruiting body composed of several genetically different clones, taxation problem arises. Stalk can be regarded as "common property" that works to increase the utility of "private property", spores. The problem that must be solved is "How many cells of each clone should differentiate into stalk cells?". Because stalk cells can be regarded as tax, this problem can be rephrased as "How much should each clone contribute to common property by paying tax?". In the biological world, all the problems must be solved evolutionarily. Thus we try to find the solution to the problem by obtaining the evolutionarily stable stalk ratio of each clone, which will be achieved by adaptive evolution.

EVOLUTIONARILY STABLE STALK RATIO

We consider a fruiting body consisting of m clones. We denote by x_i and y_i , respectively, the total number of cells and the number of spore cells belonging to clone i ($i = 1, 2, \dots, m$) in the fruiting body. The number of stalk cells of clone i is $x_i - y_i$. We also denote by ϕ_i the fitness or the expected number of surviving offspring of clone i . For convenience, we denote by y the total number of spore cells ($\sum_{j=1}^m y_j$), and by x the total

number of cells ($\sum_{j=1}^m x_j$). Total number of stalk cells is $x - y$. Let $y = (y_1, y_2, \dots, y_m)$. The fitness of clone i is

$$\phi_i = y_i f(y, x), \quad (1)$$

because the survival probability of a spore is determined by the size of the fruiting body and the size of the stalk. The function f increases with increasing stalk size, $x - y$, because spore dispersal is improved by a large stalk.

A necessary condition for $y^* = (y_1^*, y_2^*, \dots, y_m^*)$ to be evolutionary stable is

$$\begin{aligned} \frac{\partial \phi_i}{\partial y_i} &= f + y_i^* \frac{\partial f}{\partial y_i} = 0 \\ \Leftrightarrow y_i^* &= - \frac{f}{\partial f / \partial y_i} \end{aligned} \quad (2-a)$$

and

$$\frac{\partial^2 \phi_i}{\partial y_i^2} = 2 \frac{\partial f}{\partial y_i} + y_i^* \frac{\partial^2 f}{\partial y_i^2} \leq 0 \quad (2-b)$$

for i that satisfies $y_i^* > 0$, and

$$\begin{aligned} \frac{\partial \phi_i}{\partial y_i} &= f + y_i^* \frac{\partial f}{\partial y_i} > 0 \\ \Leftrightarrow y_i^* &< - \frac{f}{\partial f / \partial y_i} \end{aligned} \quad (2-c)$$

for i that satisfies $y_i^* = x_i$ (these derivatives are all at $y = y^*$). This means that clone i cannot do better by changing its stalk ratio. Because $\frac{\partial f}{\partial y_i} = \frac{df}{dy}$, the right hand sides of (2-a) and (2-c) are common to all i . A clone produces both stalks and spores if its size, x_i , is larger than a critical size, $y_c = -f / (\partial f / \partial y)$, and produces spores alone if it is smaller. Moreover, the number of spores produced by a clone larger than the critical size is y_c and is independent of clone size. Thus the fitness of clones larger than

the critical size are equal; the larger clones do not necessarily enjoy higher fitness than the smaller ones. Evolution of the clones trying to maximize its self-interest will lead to the more progressive taxation rate than income tax, and finally to the equalization of private property (net income). Thus we call this as "the law of equalization in net income".

The prediction of the present analysis seems to be easily testable by marking cells of a clone, mixing them with other clones in various ratio and letting the mixture form a fruiting body. However, there is no experimental study on the differentiation ratio of individual clones in the multi-clonal fruiting body. So far, we cannot find any experimental support for our prediction.

In addition to the analysis shown above, we studied the evolutionarily stable stalk ratio (ESSR) of cellular slime molds in more detail (Matsuda and Harada, in press). We obtained the condition for ESSR to be independent of fruiting body size and discussed other properties of ESSR such as those equivalent to "the tragedy of commons" (Hardin 1968), evolutionarily stable number of co-aggregating clones and the conflict between large and small clones. Interested readers should consult Matsuda and Harada (in press).

EQUALIZATION IN INVESTMENT

There are some species, other than cellular slime molds, in which individuals are reported to allocate equal amount of reproductive investment on a component of reproductive allocation even if there is variation among individuals in total reproductive investment. For example, Yamaguchi(1985) reported that sexuparae of an aphid, *Prociphilus oriens*, produce equal number of sons; a larger sexupara with large reproductive investment produces a larger number of daughters than a smaller one, but produces the same number of sons as a smaller one. Hiratsuka (1989) showed that individuals of a Polygonaceous plant, *Polygonum Thunbergii*, produce equal number of cleistogamic (closed) flowers; a large plant produces a larger number of chasmogamic (open) flowers, but produces the same number of cleistogamic flowers as a smaller one. In these situations, we cannot regard one component as private property and the other as common property. Thus it seems that we must treat these phenomena in the frame work different from that of

cellular slime molds. Mathematically, however, these situations have similar structures to the previous cellular slime mold case as shown below, and, by clarifying the ecological significance of this structure, we may be able to get a clue to treat broader range of ecological problems in the same frame work.

Yamaguchi (1985) explained the sex allocation of the aphid by analyzing a simple mathematical model as follows. Consider that mating takes place between offspring of m sexuparae; sons of m sexuparae compete locally for the access to the daughters of those sexuparae. In this situation, the fitness of a sexupara i is

$$\phi_i = r \frac{y_i}{y} (x - y) + r (x_i - y_i) \quad , \quad (3)$$

where x_i and y_i are the total reproductive investment and the investment to sons, respectively, of a sexupara i . $y = \sum_{j=1}^m y_j$ and $x = \sum_{j=1}^m x_j$, r is a

positive constant. $x - y$ is the total investment to daughters and $\frac{y_i}{y}$ is the proportion of daughters that are inseminated by sons of sexuparae i . Thus the first term expresses the fitness increment through sons and the second expresses that through daughters. A Nash non-cooperative equilibrium in this case is

$$\begin{aligned} y_i^* &= y_c & \text{for } \{i: x_i > y_c\} \\ y_i^* &= x_i & \text{for } \{i: x_i \leq y_c\}, \end{aligned}$$

where

$$y_c = y^* \left(1 - 2 \frac{y^*}{x}\right) .$$

What produced the similarity between the cellular slime molds and the aphid? It can easily be seen that, in both cases, the fitness is written as

$$\phi_i = y_i f(y, x) + c(x_i - y_i) \quad , \quad (4)$$

where $f(y, x)$ is a decreasing function of y and c is a constant. In the cellular slime molds, f is the survival probability of a spore and $c = 0$. In the aphid, $f = r \frac{x-y}{y}$ and $c = r$. $f(y, x)$ and c are per capita fitness increment through each component of investment. Thus (4) implies that per capita fitness increment through the investment on one component depends on the total amount of resource invested to that component, but that through the investment on the other component is independent. We can easily show that there exists a Nash equilibrium that satisfies

$$y_i^* = y_c \quad \text{for } \{i: x_i > y_c\} \quad (5-a)$$

$$y_i^* = x_i \quad \text{for } \{i: x_i \leq y_c\} \quad (5-b)$$

or

$$y_i^* = 0 \quad \text{for all } i \quad (5-c)$$

for some $y_c > 0$, if f is a continuously differentiable decreasing function of y (Appendix). This can be regarded as an extension of the law of equalization in net income.

Flower production of *Polygonum Thunbergii* is another example of the extended law. Cleistogamic flowers produce non-dispersing seeds which germinate at the place they are produced and compete with non-dispersing seeds produced by neighboring plants. Thus their fitness decreases as the number of cleistogamic flowers produced in the neighborhood increases. Per capita fitness increment through investment on the cleistogamic flowers depends on the total investment by the neighboring plants on that type of flowers. On the other hand, Chasmogamic flowers produce dispersing seeds whose fitness is not affected by the local production of dispersing seeds. Therefore, the fitness of a plant is expressed as (4), where y_i is investment on cleistogamic flowers, which implies equalization of the production of cleistogamic flowers at the Nash equilibrium.

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APPENDIX

In this appendix, we show that there exists a Nash equilibrium that satisfies

$$y_i^* = y_c \quad \text{for } \{i: x_i > y_c\}, \quad (5-a)$$

$$y_i^* = x_i \quad \text{for } \{i: x_i \leq y_c\} \quad (5-b)$$

or

$$y_i^* = 0 \quad \text{for all } i, \quad (5-c)$$

if the fitness of individual i is

$$\phi_i = y_i f(y, x) + c(x_i - y_i), \quad (4)$$

where f is a smoothly differentiable decreasing function of $y (= \sum_{j=1}^m y_j)$, c is a positive constant and y_i represents strategy of individual i that is constrained by $0 \leq y_i \leq x_i$. Define $x = \sum_{j=1}^m x_j$, $y = (y_1, y_2, \dots, y_m)$ and $\mathbf{x} = (x_1, x_2, \dots, x_m)$. Assume without losing generality that $x_1 \geq x_2 \geq \dots \geq x_m$.

From (4),

$$A1: \quad \frac{\partial \phi_i}{\partial y_i} = f(y, x) + y_i \frac{\partial f}{\partial y} - c,$$

which implies

$$A2: \quad \frac{\partial \phi_i}{\partial y_i} \geq \frac{\partial \phi_j}{\partial y_j} \Leftrightarrow y_i \leq y_j$$

and

$$A3: \quad \frac{\partial \phi_i}{\partial y_i} \text{ takes the global maximum at } y=(0, 0, \dots, 0), f(0, x) - c.$$

If $f(0, x) < c$, then

$$\frac{\partial \phi_i}{\partial y_i} < 0$$

is globally satisfied and $y = (0, 0, \dots, 0)$ is a Nash equilibrium that satisfies (5-c).

If $f(0, x) > c$, there are two possibilities. If $\frac{\partial \phi_1}{\partial y_1} > 0$ at $y = \mathbf{x}$, then,

from A2, $\frac{\partial \phi_i}{\partial y_i} > 0$ is satisfied for all i at $y = \mathbf{x}$. Thus $y = \mathbf{x}$ is a Nash equilibrium that satisfies (5-b) in which y_c is set to be larger than x_1 . If $\frac{\partial \phi_1}{\partial y_1} \leq 0$ at $y = \mathbf{x}$, we can show that there exists a Nash equilibrium that satisfies (5-a) and (5-b) as follows. Define a vector valued function $\mathbf{z}(t) = (z_1(t), z_2(t), \dots, z_m(t))$, where

$$\begin{aligned} z_i(t) &= t && \text{for } \{i: x_i \geq t\} \\ z_i(t) &= x_i && \text{for } \{i: x_i < t\} \end{aligned}$$

Then, by A1,

$$\begin{aligned} \frac{\partial \phi_i}{\partial y_i} \Big|_{y=z(t)} &= \frac{\partial \phi_j}{\partial y_j} \Big|_{y=z(t)} && \text{for } \{i, j: x_i \geq t, x_j \geq t\} \\ \frac{\partial \phi_i}{\partial y_i} \Big|_{y=z(t)} &\leq \frac{\partial \phi_j}{\partial y_j} \Big|_{y=z(t)} && \text{for } \{i, j: x_i \geq t, x_j < t\} \end{aligned}$$

Thus, by the continuity of $\frac{\partial \phi_i}{\partial y_i}$ and A2, there exists t^* such that, for $\{i: x_i$

$\geq t^*\}$, $\frac{d\phi_i}{dy_i} \Big|_{y=z(t)}$ changes sign from minus to plus at $t = t^*$ as t is continuously decreased, and, for $\{i: x_i \geq t^*\}$,

$$\frac{d\phi_i}{dy_i} \Big|_{y=z(t^*)} > 0$$

This implies that

$$\begin{aligned} y_i &= y_c && \text{for } \{i: x_i \geq t\} \\ y_i &= x_i && \text{for } \{i: x_i < t\} \end{aligned}$$

is a Nash equilibrium, if we define $y_c = t^*$.

In the case of cellular slime molds,

$$c = 0 \leq f(0, x).$$

Thus there exists a Nash equilibrium that satisfies (5-a) and (5-b), which implies "the law of equalization in net income".